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Impacts of livestock in regenerating upland birch woodlands in Scotland

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Abstract

Including large herbivores in wooded areas is often seen as a useful conservation tool. Browsing intensities on saplings in seven upland birch woodlands grazed by sheep, cattle and wild herbivores were studied. The aims were to determine whether tree regeneration could occur in the presence of livestock, particularly sheep, and the conditions under which stock can be grazed sustainably within woodlands.

The results showed that regeneration can occur at sites grazed by livestock. Within-site variation in the proportion of shoots browsed per sapling was high, but significant trends were detected. Browsing intensity was negatively related to good quality biomass per livestock unit, basal diameter and adjacent vegetation height. Saplings with a topiaried growth form were browsed more than saplings with a normal growth form.

When writing management plans, stocking densities should be set in relation to forage quantity and quality. Understanding the relationship between good quality biomass per livestock unit and browsing intensity will facilitate more sustainable management of grazing within woodlands.

Keywords: Browsing intensity; Sheep; Cattle; Natural regeneration; *Betula*

1. Introduction

Birch (*Betula pubescens*, *Betula pendula*) is an important component of boreal forests throughout NW Europe (Bradshaw and Edenius, 1998). In Scotland, birch woodlands cover less than 2 % of the area of the uplands (Milne et al., 1998) and are important for their landscape and biodiversity value (Fenton, 1984; Forestry Commission, 1994) and for the shelter they provide to domestic stock (Hulbert et al., 1999). The presence of grazing herbivores in woodlands is thought to be beneficial to woodland flora by enhancing structural complexity (Hester and Miller, 1995; Mayle, 1999; Bengtsson et al., 2000), facilitating tree seedling establishment through disturbance of the ground vegetation, and reducing competition between seedlings and ground flora (Miles and Kinnaird, 1979). However, excessive grazing in woodlands (as in other habitats) can cause deleterious changes through reduction in structural complexity and species richness (Kuiters and Slim, 2002; Mysterud and Østbye, 2004; Anderson and Radford, 1994; Summers et al., 1997; Milne et al., 1998; Milner et al., 2002). Critically, the intensity of browsing impact determines whether woodlands regenerate and are sustainable.

In Scotland, the introduction of extensive sheep farming methods in the late 1700s (Ritchie, 1919) and high numbers of deer (Miles and Kinnaird, 1979) have been blamed for the paucity of woodland remaining in the uplands. While grazing animals can and do suppress tree regeneration, the woodland area was probably much reduced before extensive sheep farming began (Stewart, 2003; Tipping, 2003; Smout, 1997).

Unlike red (*Cervus elaphus*) and roe (*Capreolus capreolus*) deer, sheep (*Ovis aries*) and cattle (*Bos taurus*) are primarily grazers rather than browsers (Hofmann, 1989; Mitchell and Kirby, 1990; Putman et al., 1989). However, both sheep and cattle will browse on small trees and woody shrubs (Hester et al., 1996; Pitt et al., 1998; Lombardi et al., 1999; Tolhurst and Oates, 2001). Only two published studies have investigated the effects of different grazing treatments on tree regeneration in the UK (Hester et al., 1996; Welch, 2003). Moreover, there is no information on the selection preferences of sheep and cattle in open woodland habitats where choices are between grassland, heather moorland or regenerating tree saplings.

In Scotland, upland birch woodlands are usually unfenced since they lie above the areas enclosed for more intensive production. The woodlands are open to other habitats, usually moorland, either dry- or wet-heath, but occasionally semi-improved grassland. Young trees (when present) are found in the habitats adjacent to woodlands, as birch seldom regenerate under their own canopy (Atkinson, 1992).

Although young birch are able to tolerate some shoot and foliage loss (Millard et al., 2001; Anttonen et al., 2002; Hester et al., 2004) high intensities of browsing reduce growth rates (Hester et al., 1996) and can increase mortality (Kinnaird, 1974). Suppressed birch saplings aged 16 years but with a dwarfed stature and little annual growth have been observed (Kinnaird, 1974). This ‘topiary’ effect (Rackham and Moody, 1996) results in trees with short, wide stature, contorted stems and highly branched canopies.

UK forestry grant schemes for planted trees and natural regeneration typically required livestock and deer exclusion from both establishing and mature woodlands (Forestry Commission, 2001; Forestry Commission, 2003). However, both farmers and conservationists would usually prefer not to completely exclude stock from woodlands. Farmers view woodlands with a long history of grazing as an intrinsic part of the grazed area of the farm, while conservationists view stock exclusion as undesirable for woodland structure, biodiversity and seedling establishment (Kirby et al., 1994; Humphrey, 1998; Mayle, 1999).

There are very few guidelines on the stock management or density required to meet different management objectives (Hester et al., 2000). Anecdotal recommendations of deer densities that should allow tree regeneration have been made (e.g. approximately 5 deer km⁻², Miller et al., 1982). However, these recommendations do not take into account alternative forage and may not be applicable to domestic stock, which are expected to consume a smaller proportion of browse than deer (Hofmann, 1989; Mitchell and Kirby, 1990). Successful management requires greater understanding of the impact of domestic herbivores on tree regeneration.

The work reported is an observational study of several sites where upland birch woodlands were regenerating in the presence of domestic livestock as well as wild herbivores (red and roe deer and hares (*Lepus capensis*, *L. timidus*)). The aims were to evaluate whether tree regeneration could occur in the presence of livestock, particularly sheep, and to determine the site factors and sapling characteristics that influence browsing intensity. The hypotheses to be tested

were that browsing intensity is dependent on: 1) livestock species and stocking density; 2) stocking density relative to forage availability; 3) characteristics of saplings (height, span, growth form, shoot number, height of adjacent vegetation, distance to neighbouring saplings).

2. Methods

2.1. Study sites

Seven regenerating semi-natural birch woodlands in the west-central Highlands of Scotland were selected (Fig. 1). The sites were grazed by sheep, or sheep and cattle, plus wild herbivores (red deer, roe deer and hares) (Table 1). Interviews with the owner or manager of each site determined the grazed area (including the woodland and all ground open to it) and the number, type and seasonal grazing regime of stock present at the site (Table 2). The distribution of habitat types within sites varied considerably (Fig. 2). Most sites had extensive rough grazing dominated by *Calluna vulgaris*, *Erica tetralix* or *Molinia caerulea*, and little semi-improved grassland.

Stocking density was measured in Livestock Unit days per hectare (LU days ha⁻¹). Cattle and sheep numbers were converted to LU days by assuming that: one ewe = 0.08 LU; one cow = 0.65 LU (Chadwick, 1997; Ministry of Agriculture, Fisheries and Food, 1977); one month is 30 days long (Table 2). These livestock units are defined in terms of feed requirements (Chadwick, 1997; Ministry of Agriculture, Fisheries and Food, 1977) and are different to those used for European livestock subsidy purposes (EC Council Regulation No. 1254/99).

Representative sample areas (average size 5 ha) of open ground, regenerating woodland and mature woodland were selected and their ground flora classified as grassland or heath. Dung counts were made in each of the

three sample areas by walking eight 100×1.5 m transects, counting sheep, cattle and deer pellet groups (one pellet group = at least six faecal pellets for sheep and deer, and one cow-pat for cattle (Latham et al., 1996)) and converting to pellet groups per ha. The dung counts were conducted once in September. The presence of lagomorph dung was noted but not quantified.

2.2. Browse estimates and tree characteristics

Betula pendula and *B. pubescens* saplings were not differentiated as distinguishing the two is difficult and hybrids sometimes occur (Atkinson, 1992). However, the species of mature birch at each site were noted (Table 2). One transect (5 – 15 m long) was set up per regeneration patch. Distances between patches within sites ranged from 20 m (Calvine) to 200 m (Corrimony). At most sites, five transects of 10 saplings were marked with numbered tags but at two sites where regeneration was limited three transects of five saplings were marked. The saplings selected were less than 1.5 m tall but were taller than the surrounding vegetation. The height, span and basal diameter of all saplings were measured, and the height and type of vegetation immediately adjacent to the sapling were recorded.

Saplings were classified by growth form as ‘Normal’, ‘Intermediate’ or ‘Topiaried’ (Rackham and Moody, 1996). Topiaried saplings have a very contorted stem and increased branching throughout the canopy; intermediate saplings have a somewhat contorted stem with few signs of increased branching; normal saplings have no stem contortion and no sign of increased branching.

Browsing was recorded at leaf-fall (November) and bud-break (May). For non-topiaried saplings, browsing intensity was estimated by counting the number of intact long-shoots and the number of recently browsed long-shoots (i.e. shoots browsed within the last 6 months). Long shoots were defined as live woody shoots of one year old or less bearing many daughter buds and having the potential to increase by several centimetres in a growing season (Jones and Harper, 1987). For topiaried saplings, browsing intensity was estimated by counting the number of browsed and un-browsed long shoots in three 10 x 10 cm samples (one at the top of the sapling, one on the side and one at the base). It was not possible to distinguish between browsing by the different herbivore species present.

Due to the difficulty of distinguishing between shoots browsed within the last six months and shoots browsed during the six months prior to this, the main analysis used an estimate of the annual proportion of long shoots browsed, i.e. the maximum number of browsed shoots recorded for that sapling in the two surveys divided by the maximum total number of shoots recorded.

2.3. Sward forage availability

‘Good quality forage’ biomass, sward material assumed to be of high nutritional quality, was estimated as follows (Fig 3). In each sample area of open ground, regenerating woodland and mature woodland, vegetation was sampled if the area was graminoid dominated; forage availability was not recorded if the area was heath dominated as heath species have low digestibility relative to

graminoids (Grant, 1971). Standing biomass in September was sampled by cutting twelve 1 m long \times 10 cm wide quadrats using electric lawn clippers, just above the litter layer. Each cut was approximately 7 m distant from the previous. In the laboratory, twigs were removed and proportions of live and dead sward material, leaf litter and bryophytes estimated by eye (Frame, 1993). The sample was oven-dried (80 °C) and weighed, and the estimated weights of each component, based on the proportion in the sample, converted to g m^{-2} . One hundred and twenty sward heights were measured using a HFRO sward stick (Barthram, 1986) in the locality of the biomass cuts. Vegetation height and whether the hit was to bryophyte, forb, fine-leaved grass, broad-leaved grass, *Molinia caerulea*, sedge, rush, dwarf shrub or bare ground were recorded.

The good quality biomass within each quadrat was estimated as the proportion of hits to fine-leaved grass, broad-leaved grass and forbs, multiplied by live vascular biomass (kg m^{-2}). The averaged quadrat values were multiplied up to estimate good quality biomass in each of the habitat types (open ground, regenerating woodland and mature woodland). The values for each habitat type were summed to produce good quality biomass totals for sites.

2.4. Statistical analysis

A Generalised Linear Mixed Model (GLMM) in Genstat 6 (Genstat 6.1 Committee, Rothamstead, UK) with binomial distribution and logit link function (McCullagh and Nelder, 1989) was used to model the number of shoots browsed out of the total number of shoots. It identified the factors accounting for the

greatest variation between sites and saplings. The individual sapling characteristics fitted as fixed effects were: height; span; basal diameter; distance to nearest neighbour; height of adjacent vegetation; whether or not the sapling was topiaried. The site-level variables fitted were: sheep LU days; total LU days (i.e. sheep plus cattle LU days); good quality biomass per LU day; total biomass per LU day; deer dung quantity. Transect nested within site was fitted as the random effect, reducing the influence of between-transect and between-site differences (Milner et al., 1999). A step-wise method was used to generate a minimal model containing only significant terms. The order in which terms were introduced to the model did not influence the results.

The regression model generated by the GLMM (Table 3) was used to predict proportions of shoots browsed for different values of good quality biomass per LU day, height of adjacent vegetation and sapling growth form (topiaried/non-topiaried) with basal diameter held constant at the average value (1.2 cm). To make predictions the parameter estimates were back-transformed using equation 1:

$$\text{Eqn. 1. } P = \frac{e^{(c+m_1x_1+m_2x_2+.....m_nx_n)}}{1 + e^{(c+m_1x_1+m_2x_2+.....m_nx_n)}}$$

Where P is the probability of browsing, c is the intercept, m_1 is the slope of the first parameter, x_1 is the value of the first parameter, and so on. Predictions were made for different values of basal diameter but the effects were very small compared to good quality biomass per LU day and height of adjacent vegetation.

3. Results

3.1. Site factors and tree characteristics determining browsing intensity

Good quality biomass per LU day, height of adjacent vegetation, basal diameter and whether or not saplings were topiaried significantly affected the proportion of shoots browsed (Table 3). The proportion of shoots browsed declined with increasing good quality biomass per LU day, height of adjacent vegetation and basal diameter. Topiaried trees had a greater proportion of shoots browsed than non-topiaried trees (Fig. 4). No other individual tree characteristics, such as height or span, had significant effects on browsing intensity. Where vegetation adjacent to trees was over 40 cm (Fig. 4) browsing was always under 50 %, but where adjacent vegetation was under 40 cm tall, the proportion of shoots browsed ranged from all to none. The other site level characteristics, total biomass per LU day, sheep LU days, total LU days and deer dung quantity were not significant.

There was considerable difference between total biomass per LU day and good quality biomass per LU day at two of the sites, Corrimony and Glen Stockdale (Table 4). At Corrimony, the sward contained a high proportion of moss, and at Glen Stockdale the sward contained a high proportion of dead material.

Evidence of deer was observed at all sites, and lagomorphs at four (Table 5). Deer dung density was weakly correlated with browsing intensity ($R = 0.06$), and deer dung was not a significant explanatory variable in the GLMM. The density

of sheep dung (measured in September) was weakly correlated with summer stocking density of sheep ($R = 0.44$) while for cattle the correlation was stronger ($R = 0.75$). Wild herbivore browsing may account for some of the between site variation.

There was considerable variation in the proportion of shoots browsed both within and between sites (Fig. 4; Fig. 5). All sites except Easter Tulloch had some un-browsed trees. The frequency distributions of proportion of shoots browsed varied considerably between sites (Fig. 5). At five of the sites, all trees had lost their leader in the past. At Glen Elchaig and Calvine only 4 % of trees had never lost their leader. A small proportion of leader losses may be due to causes other than browsing by large herbivores (e.g. weather, field voles (*Microtus agrestis*)). At Easter Tulloch all trees measured were topiaried, as were the majority at Laggan; at the other sites topiaried trees were absent. Topiaried trees had a larger basal diameter and were wider and taller than non-topiaried trees (Table 6).

3.2. Model predictions

The model predictions (Fig. 6) highlight the difference in browsing intensity expected for topiaried and non-topiaried trees, and that browsing is expected to be greater where vegetation is short. Information in the literature suggests that *B. pendula* saplings can tolerate 25 % defoliation (Anttonen et al., 2002). If 20 % shoot loss, a more conservative value, is taken as a guide for acceptable damage likely to permit regeneration, the model predicts that more than 10 kg per

LU day of good quality biomass is required where vegetation adjacent to normal trees is short (Fig. 6).

4. Discussion

This is the only study of browsing intensities on saplings by domestic stock in upland Scotland. We show that regeneration in the presence of sheep does occur, although tree growth form is often compromised. Browsing intensity was low where good quality biomass per LU was plentiful, and *vice versa*.

Solely using animal numbers or densities without reference to site characteristics is not a helpful approach (Pakeman et al., 2003) especially where sites are very varied. Forage quality as well as quantity must be considered when attempting to understand patterns of offtake. This work demonstrates a way to use estimates of late-summer standing green vascular biomass (i.e. good quality forage) to predict risk of browsing damage for a given stocking density. Caution should be exercised when applying the results to other sites; some of the data used has inherent variation that may have biological impacts, e.g. season and duration of grazing and group size of animals.

The predicted proportions of shoot browsing are means and there is wide variation in proportion of shoots browsed within sites (Fig. 4; Fig. 5). This should be borne in mind when using predictions; some saplings at a given site can remain un-browsed while others experience almost total shoot loss over the course of a year.

Applying appropriate livestock grazing regimes to conservation areas will enable the development of landscapes with a mosaic of different habitats whilst maintaining agricultural management and statutory requirements for animal welfare. An understanding of the relationship between herbivore population size, available forage and browsing levels will help to inform herbivore management for a range of goals, from timber production (Bradshaw and Edenius, 1998) to maintenance of open-ground habitats (Lombardi et al., 1999; Bullock and Pakeman, 1997).

If a tree repeatedly loses its highest shoot, it will develop a topiaried form (Rackham and Moody, 1996). We found topiaried trees were browsed more heavily than non-topiaried trees in similar situations. Similar findings have been reported for deer browsing on Sitka spruce (*Picea sitchensis*) (Duncan et al., 1998). It would be useful to understand the chronic intensity of browsing that forces saplings into topiaried bush-like forms, since this is also the threshold that determines whether regenerating trees will develop into high canopy woodland or remain as low scrub.

The seasonal pattern of stock presence is likely to have implications for the success or otherwise of regeneration. It would be expected that both herbivore selection for tree browse (Palmer and Truscott, 2003) and the ability of trees to re-grow following browsing (Welch, 2003; Millard et al., 2001) vary with season. Further work is required to determine if shoot loss in certain seasons influences the survival and long-term growth of birch saplings.

4.1. Spatial aspects

It is not clear whether the low intensities of browsing found in patches of long vegetation result from herbivore avoidance of the whole patch, or whether the herbivores use the patch but the trees are protected by long vegetation. The proximity of trees to patches of good quality forage is likely to influence browsing levels. Studies into the intensity of sheep browsing on heather in grass-heather mosaics (Clarke et al., 1995; Oom and Hester, 1999; Oom et al., 2002; Hester and Baillie, 1998) found that heather closest to grass patches (good quality forage) is browsed more than heather distant from grass patches. In Australia, *Pinus radiata* seedlings are more at risk from browsing by marsupials if planted in short palatable grass than in low quality tall vegetation (Pietrzykowski et al., 2003). This aspect should be investigated further.

At one site, Laggan, a wave of successful regeneration has extended westwards for the last 50 years despite relatively high stocking levels and the presence of wild herbivores. This is probably because the high levels of ground disturbance by hooves allow dense patches of seedlings to establish. Individuals on the edge of patches are heavily browsed and become topiaried, protecting the trees at the centre of the patch (*sensu* Vera, 2000).

5. Conclusions

Stock can be grazed sustainably within woodlands for landscape or biodiversity purposes as long as the available forage is sufficient to limit the browsing impact. Different mixtures of livestock and deer appear to be feasible if the total number of animals (here converted to LU days) is within the limits set by the availability of forage at the site. It is therefore possible to set management targets determining the number of animals and length of time they should graze a site with given characteristics, in order to achieve a given mean level of browsing of regenerating trees by domestic stock. Such estimates of numbers and duration of stock access should be used for initial planning purposes and to stimulate discussion between different parties with interests in the land, with site monitoring used to adjust management as necessary.

Further research should target: 1) the intensity of browsing that leads to topiary; 2) the effect of proximity of trees to patches of good quality forage; 3) easy-to-use guidelines for managers on how to relate seasonal stocking density to forage area, species composition and site productivity. Ideally, controlled experiments where the effects of individual species of herbivore can be measured should be carried out, for both planted saplings and natural regeneration.

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Table 1

Study sites. The large mammalian grazers present were ‘S’ sheep, ‘D’ deer, ‘C’ cattle.

| Site Name | Location | Grid Reference (British National Grid) | Grazers | Years Visited | Regeneration (P = plentiful; L = limited) |
|----------------|-----------------|--|---------|---------------|---|
| Calvine | Pitlochry | NN 776 674 | S,D | 2000-01 | P |
| Corrimony | Inverness-shire | NH 340 300 | S,D | 2001-02 | P |
| Easter Tulloch | Nethy Bridge | NH 977 157 | S,C,D | 2000-01 | L |
| Glen Elchaig | Dornie | NG 942 294 | S,C,D | 2001-02 | P |
| Glen Stockdale | Appin | NM 952 487 | S,D | 2000-01 | L |
| Laggan | Badenoch | NN 657 934 | S,C,D | 2000-01 | P |
| Strathcarron | Loch Carron | NG 980 447 | S,C,D | 2001-02 | P |

Table 2

Site descriptions. The area, species of mature birch tree present (Bpe = *Betula pendula*, Bpu = *Betula pubescens*), seasonal stock numbers and stocking density at each site. Stocking density is expressed in days per ha (LU d ha⁻¹) for each species during the summer (S; May – October) and winter (W; November – April) seasons and as an annual total (A).

| Site | Area (ha) | Birch Sp. | Season | Sheep | | | Cattle | | | Total |
|-------------------|--------------|--------------|--------|--------------|-------------|-----------------------|--------------|-------------|-----------------------|-----------------------|
| | | | | No. stock | No. Days | LU d ha ⁻¹ | No. stock | No. days | LU d ha ⁻¹ | LU d ha ⁻¹ |
| Calvine | 20 | Bpe,Bpu | S | 60 | 30 | 7.2 | | | | 7.2 |
| | | | W | 60 | 150 | 36.0 | | | | 36.0 |
| | | | A | | | | | | | 43.2 |
| Corrimony | 530 | Bpe,Bpu | S | 150 | 120 | 2.7 | | | | 2.7 |
| | | | W | | | | | | | |
| | | | A | | | | | | | 2.7 |
| Easter Tulloch | 30 | Bpe,Bpu | S | | | | 40 | 150 | 130.0 | 130.0 |
| | | | W | 45 | 90 | 10.8 | 40 | 30 | 26.0 | 36.8 |
| | | | A | | | | | | | 166.8 |
| Glen Elchaig | 360 | Bpu | S | 270 | 180 | 10.8 | 25 | 180 | 8.1 | 18.9 |
| | | | W | 270 | 180 | 10.8 | 25 | 180 | 8.1 | 18.9 |
| | | | A | | | | | | | 37.8 |
| Glen Stockdale | 480 | Bpu | S | 315 | 180 | 9.5 | | | | 9.5 |
| | | | W | 315 | 180 | 9.5 | | | | 9.5 |
| | | | A | | | | | | | 19.0 |
| Laggan | 120 | Bpe,Bpu | S | 120 | 60 | 4.8 | 60 | 180 | 58.5 | 63.3 |
| | | | W | 120 | 180 | 14.4 | 60 | 180 | 58.5 | 72.9 |
| | | | A | | | | | | | 136.2 |
| Strathcarron | 440 | Bpu | S | 460 | 180 | 15.1 | 10 | 180 | 2.7 | 17.8 |
| | | | W | 460 | 180 | 15.1 | 10 | 180 | 2.7 | 17.8 |
| | | | A | | | | | | | 35.6 |

Table 3

Fixed effects explaining variation in the proportion of shoots browsed per tree over the course of one year ($n=280$), with parameter estimates and standard errors for the minimal GLMM with site/transect fitted as a random effect. Biom per LU day was the biomass of good quality forage (see methods) at a site in kg per LU day, Veg height is the height of vegetation adjacent to a sapling, Topiaried is a factor describing whether or not a tree is topiaried. p -values were estimated by assuming the Wald statistic followed a chi-squared distribution; this can underestimate p -values, which should therefore be interpreted cautiously.

| Term | Estimate | s.e | p |
|-----------------|----------|-------|--------|
| Intercept | -0.336 | 0.209 | 0.109 |
| Biom per LU day | -0.094 | 0.009 | <0.001 |
| Veg height | -0.018 | 0.005 | <0.001 |
| Basal diameter | -0.241 | 0.116 | <0.001 |
| Topiaried | 1.436 | 0.191 | <0.001 |

Table 4

Good quality and total biomass per LU day at sites

| Site | Good quality biomass per LU day (kg per LU day) | Total biomass per LU day (kg per LU day) |
|----------------|---|--|
| Calvine | 24.0 | 28.3 |
| Corrimony | 18.7 | 64.6 |
| Easter Tulloch | 8.7 | 11.1 |
| Glen Elchaig | 0.3 | 0.9 |
| Glen Stockdale | 3.3 | 56.2 |
| Laggan | 0.4 | 0.5 |
| Strathcarron | 0.9 | 2.2 |

Table 5

Dung densities for sheep, cattle and deer (red and roe) and presence of
Lagomorph (rabbit and/or hare) dung.

| Site | Dung density (pellet groups ha ⁻¹) | | | Lagomorphs |
|----------------|--|--------|------|------------|
| | Sheep | Cattle | Deer | |
| Calvine | 322 | 0 | 3 | |
| Corrimony | 139 | 0 | 39 | ● |
| Easter Tulloch | 0 | 269 | 17 | ● |
| Glen Elchaig | 328 | 128 | 64 | |
| Glen Stockdale | 236 | 0 | 25 | |
| Laggan | 581 | 33 | 36 | ● |
| Strathcarron | 325 | 42 | 69 | ● |

Table 6

Mean values of tree characteristics for topiaried and non-topiaried saplings.

| Variable | Topiaried mean (cm) | S.E. | Non-topiaried mean (cm) | S.E. |
|----------------|------------------------|------|----------------------------|------|
| Basal diameter | 2.4 | 0.01 | 0.9 | 0.05 |
| Span | 70.9 | 3.3 | 38.2 | 1.3 |
| Height | 65.5 | 1.4 | 50.15 | 3.5 |

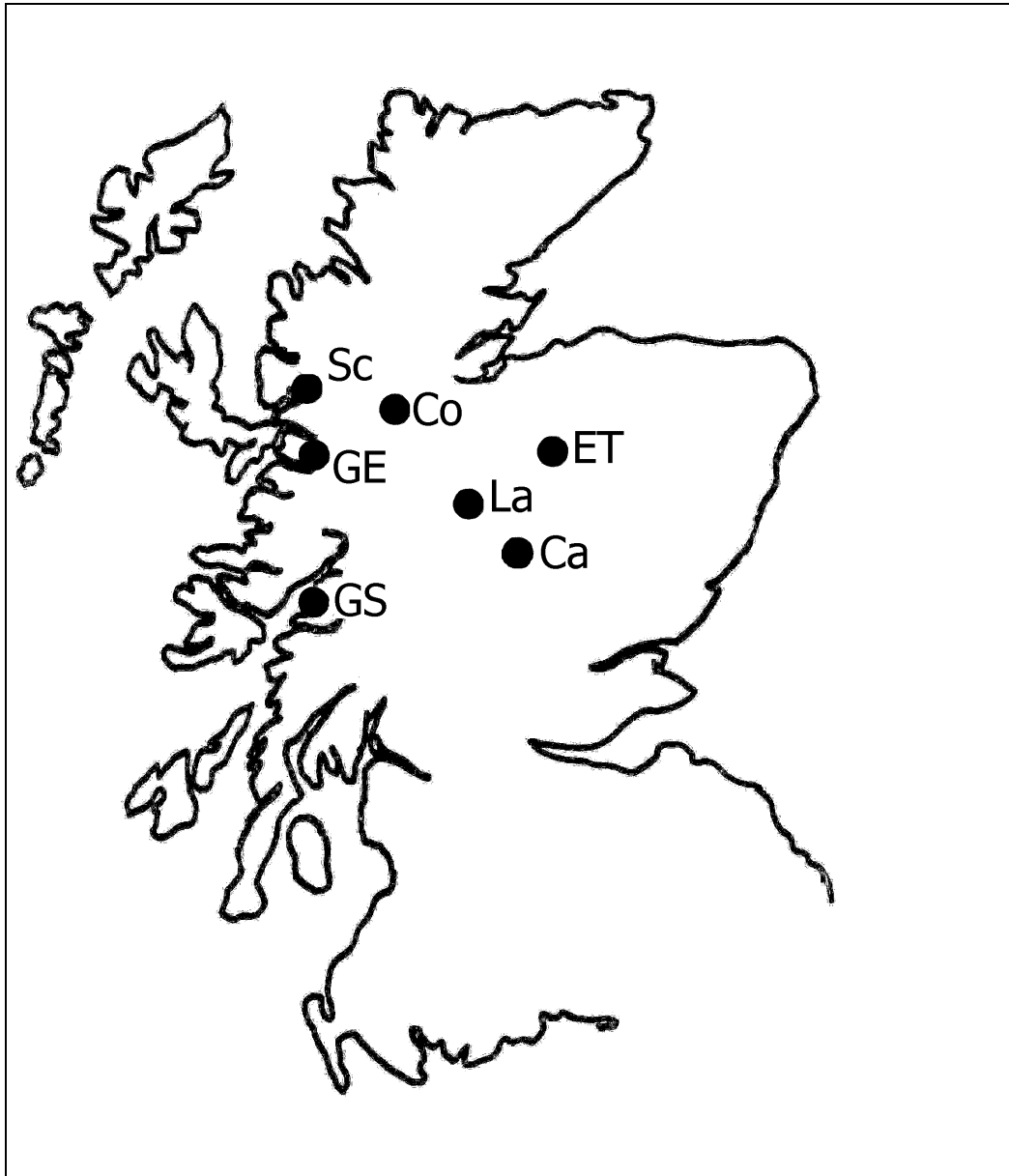


Fig. 1. Map of locations of study sites (Sc = Strathcarron; Co = Corrimony; GE = Glen Elchaig; La = Laggan; Ca = Calvine; GS = Glen Stockdale; ET = Easter Tulloch).

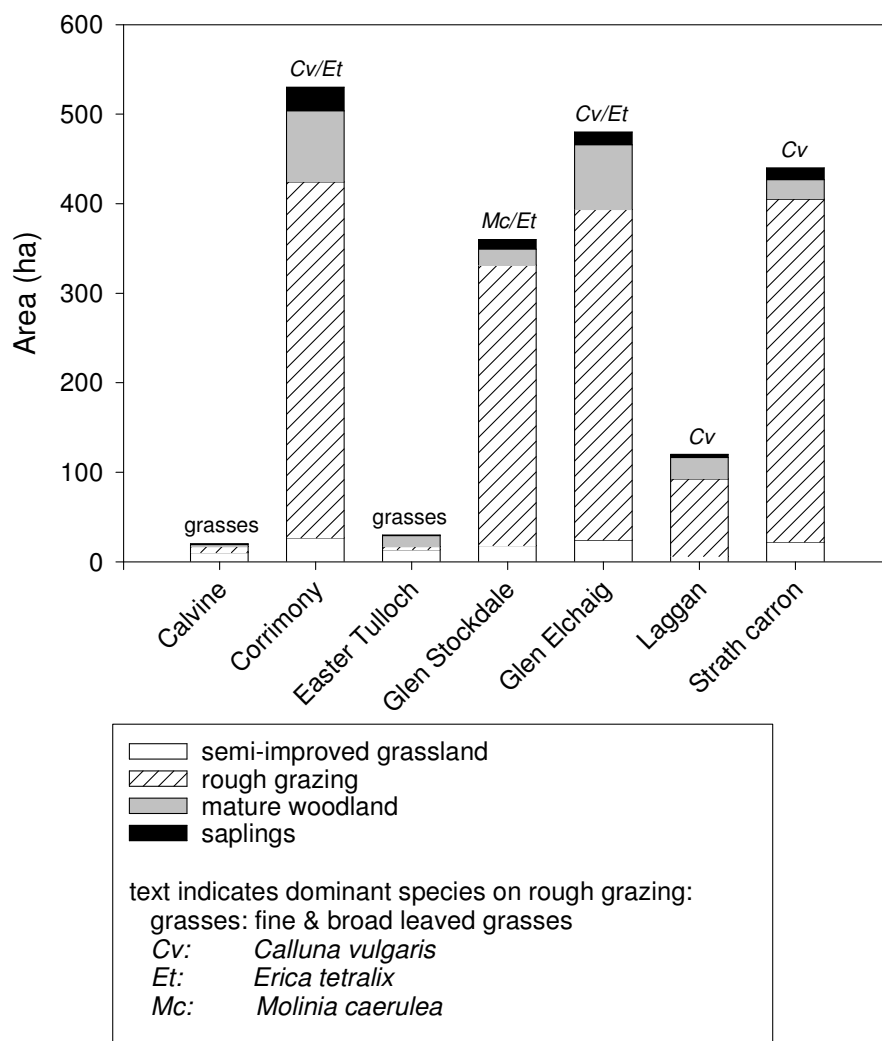


Fig. 2. Areas of habitat types and dominant species in open ground at each site.

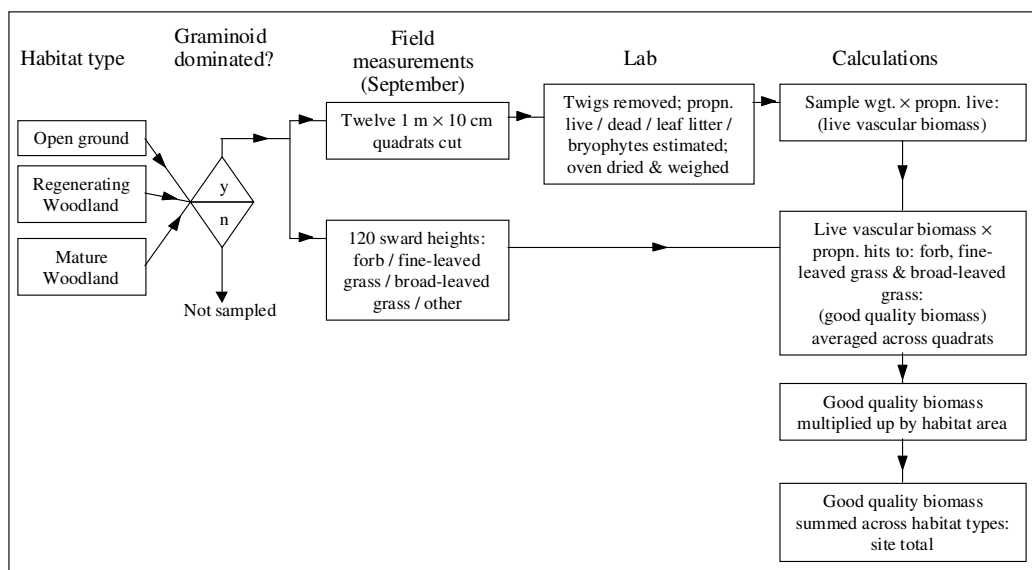


Fig. 3. Methods used to estimate biomass of good quality forage (forage assumed to be of high nutritional quality).

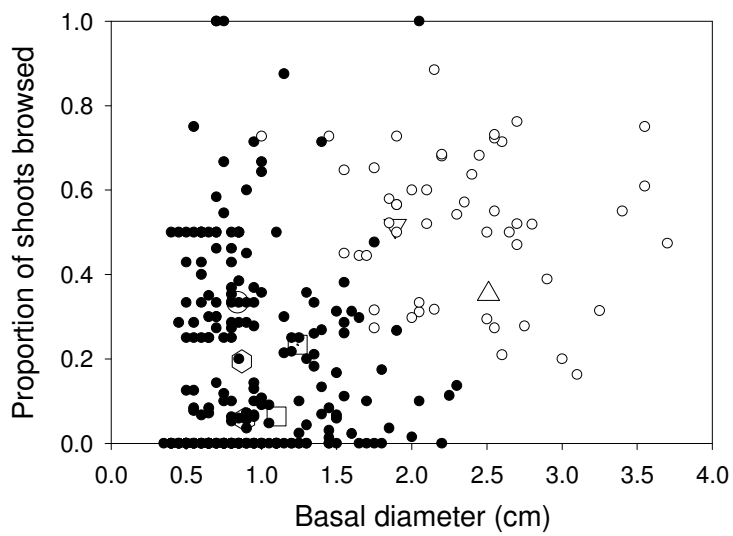
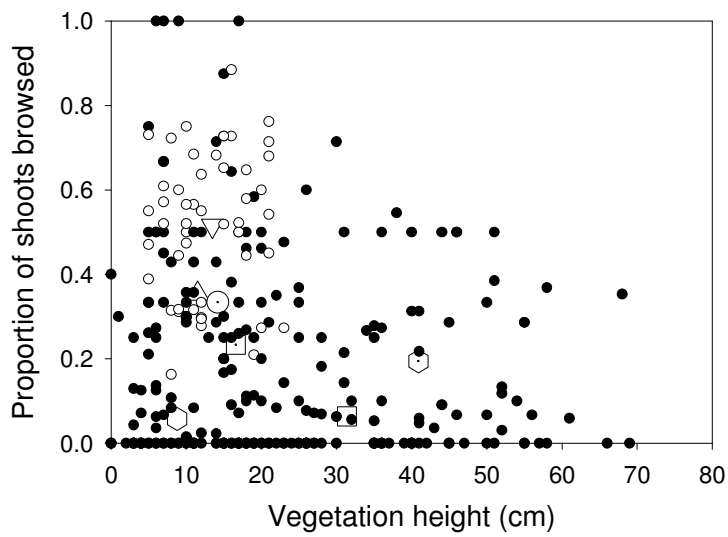
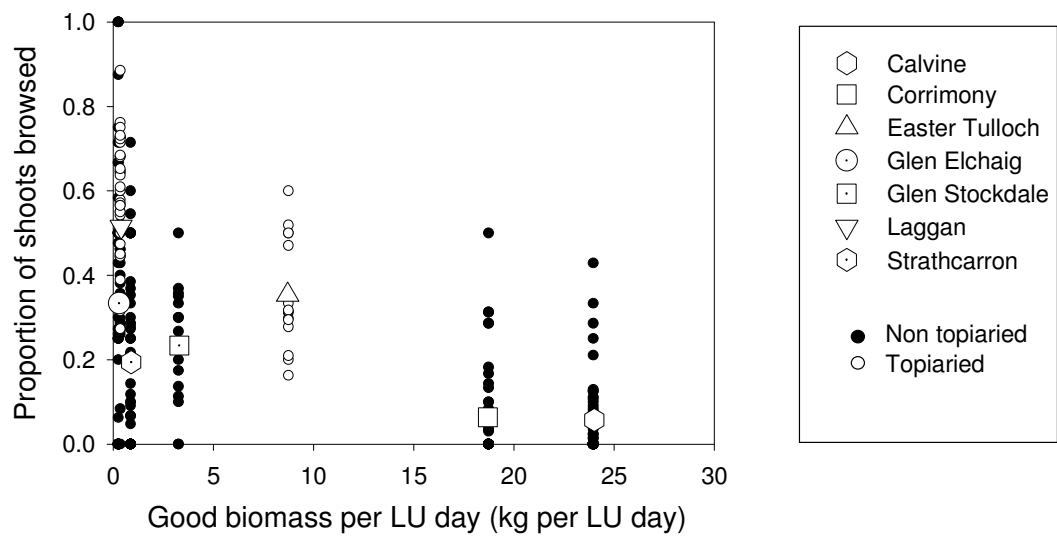


Fig. 4. Scatter diagrams of the relationship between the proportion of shoots browsed and the significant variables in the regression model: a) Good quality biomass per LU day; b) Height of vegetation adjacent to sapling; c) Basal diameter. Data are presented for individual topiaried (\circ) and non-topiaried (\bullet) saplings, and for site means (symbols in legend).

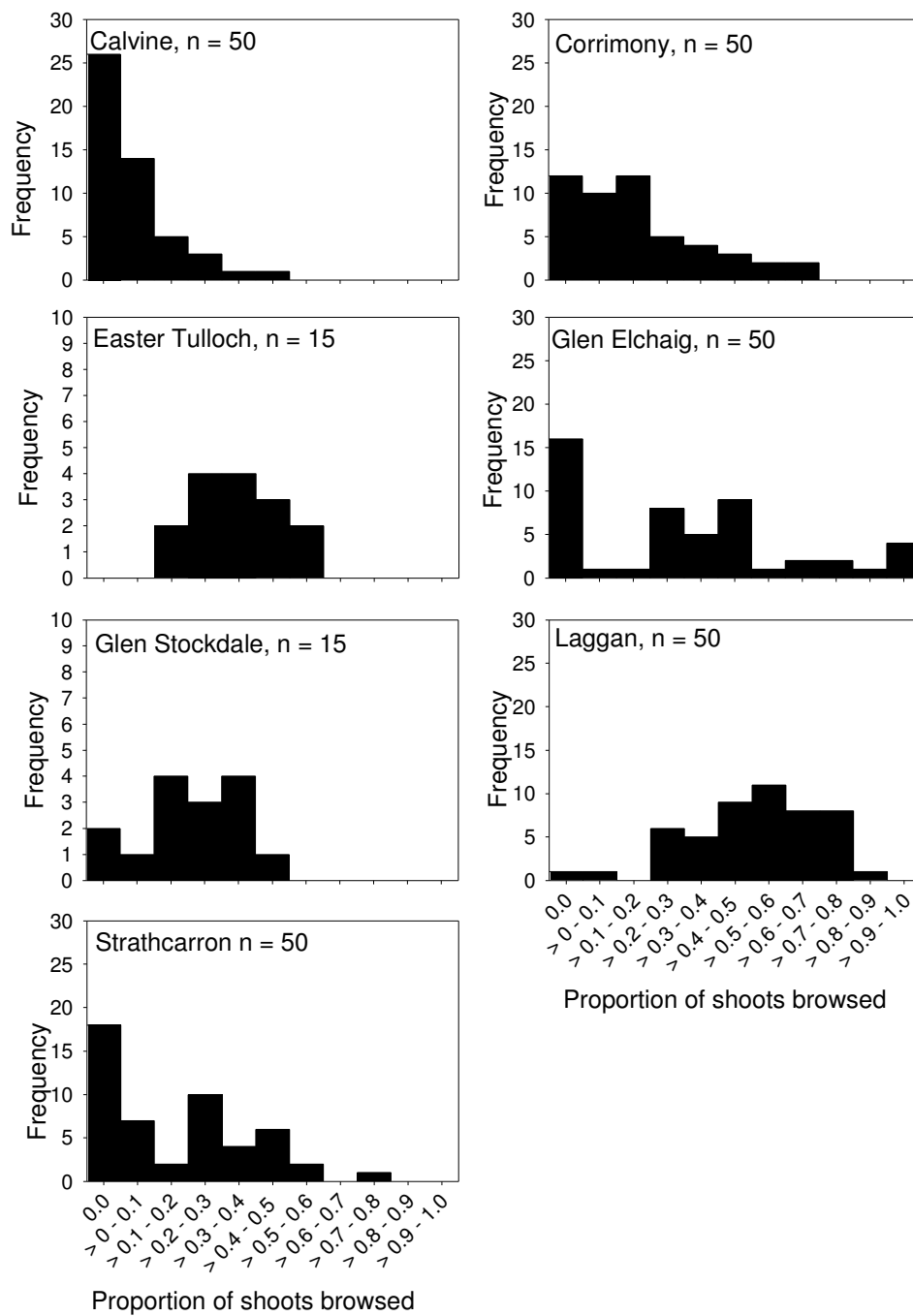


Fig. 5. Histograms of the proportion of shoots browsed during one year at each site.

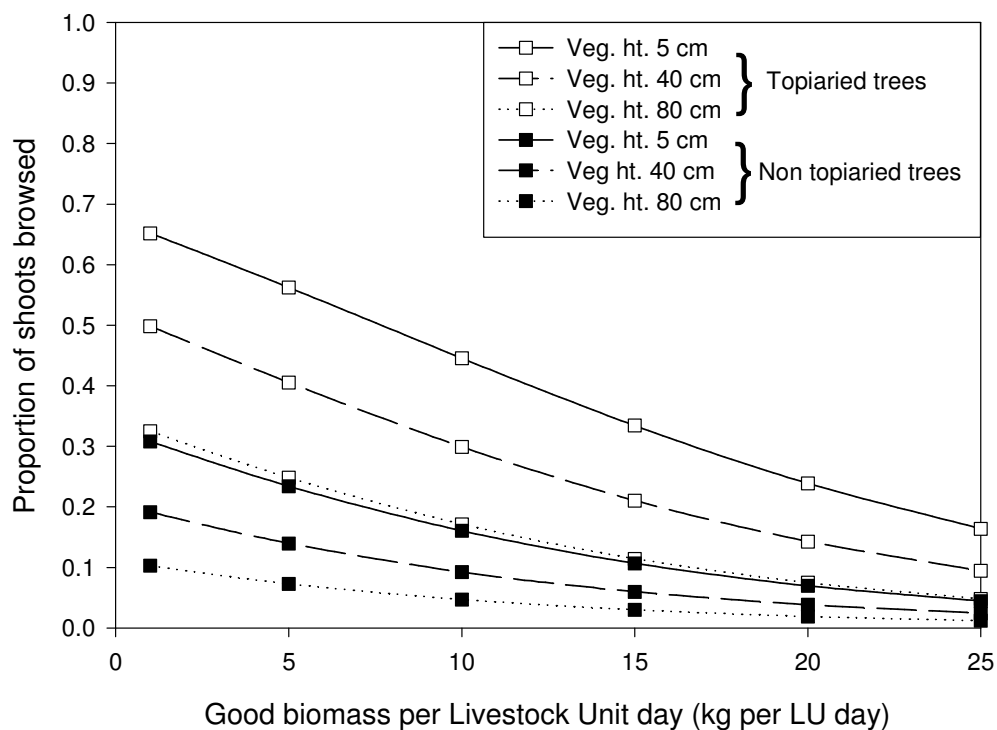


Fig. 6. Browsing intensities predicted by GLMM model for the range of good biomass per LU day from 1 to 25 kg per LU day, for topiaried and non-topiaried trees with a range of vegetation heights and for the average basal diameter (1.2 cm). The maximum standard error was 0.08, but this value should be interpreted cautiously as the model is not linear.